General and specific responses of understory vegetation to cervid herbivory across a range of boreal forests

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Understanding the responses of ecological communities to perturbation is a key challenge within contemporary ecology research. In this study we seek to separate specific community responses from general community responses of plant communities to exclusion of large cervid herbivores. Cervid herbivory and forestry are the main drivers of vegetation structure and diversity in boreal forests. While many studies focus on the impact of cervids on trees, a high proportion of the biodiversity and ecosystem services in boreal forests is found in the field layer. However, experimental approaches investigating the influence of herbivory on understory vegetation are highly localised. In this study we use a regional-scale design with 51 sites in four boreal forest regions of Norway, to investigate the influence of cervid herbivory on the physical and ecological structure of field layer vegetation. Our study sites cover a range of forest types differing in productivity, management and dominant cervid species, allowing us to identify generic responses and those that are specific to particular conditions. We found that the height of the field layer and the abundances of individual species were most susceptible to change following short-term cervid exclusion across different forest types and cervid species. Total vegetation density and vascular plant diversity did not respond to cervid exclusion on the same time scale. We also found that the field-layer vegetation in clear-cut forests used by moose was more susceptible to change following cervid exclusion than mature forests used by red deer, but no strong evidence that the response of vegetation to herbivore exclusion varied with productivity. Our study suggests that the parameters that respond to cervid exclusion are consistent across forest types, but that the responsiveness of different forest types is idiosyncratic and hard to predict.

The recent dramatic increase of many ungulate populations across Europe and North America in recent decades has sparked a major interest in their effects on biodiversity and ecosystem processes (Côté et al. 2004). The impact of cervid and forest management within boreal forests often focuses on trees for their commercial value and their influence on successional processes (Hidding et al. 2013, Speed et al. 2013a). However, a large proportion of forest biodiversity and a high proportion of boreal forest ecosystem services are found below the forest canopy, in the field and shrub vegetation layers (Gamfeldt et al. 2013). Cervids can also influence field-layer vegetation (Tremblay et al. 2006), and the effects of cervids on both the tree and field-layer can have knock-on impacts on other aspects of forest communities and ecosystems; cervids can thus be defined as keystone species (Suominen 1999) or ecosystem engineers (Rooney and Waller 2003) in boreal forests.

The key elements in our theoretical understanding of how grazing and browsing influence ecosystem responses are related to how herbivores differing in selectivity impact vegetation and how vegetation comprised of species differing in distribution along the herbivory resistance–tolerance continuum respond to herbivory (Hester et al. 2006, Evju et al. 2009). Firstly, plant community responses are expected to change both with herbivore density and selectivity, and typically this is expected to depend on whether herbivore species are mainly grazers or browsers (Gordon and Prins 2008). Changes in plant community composition in relation to varying herbivore densities are expected to develop over time driven by processes such as foraging and trampling, initially affecting vegetation structure and the relative biomass of plant species (Milchunas et al. 1988). Differences in herbivore selection pressure between plant species are likely to lead to variations in abundance, of initially highly selected species, and later species that they are in competition with (Augustine and McNaughton 1998). Secondly, species differ in functional traits that indicate their response to herbivory. For example, species with tolerance...
or resistance traits can gain a competitive advantage under heavy herbivory pressure if more competitive plants with lower defence investment or lower capacity to compensate for tissue loss are selected by the herbivores (Skarpe and Hester 2008). Therefore, the response of vegetation to herbivory will vary between sites, as the species present in different sites will vary in trait distribution due to site-specific environmental factors. Community parameters such as species richness or evenness are expected to respond on a longer time scale to herbivore exclusion as these parameters are driven by extinction and colonisation processes (Milchunas et al. 1988).

The response of vegetation to herbivory in forests also depends on factors such as successional state, productivity and climate. Changes in vegetation structure and species composition are expected to be faster in clear-cut forests compared to more mature forests where nutrient availability is low and light limiting (Tremblay et al. 2007). Additionally, more productive forests are expected to differ in response rate and even direction to less productive forests due to greater resource availability (Proulx and Mazumder 1998): the compensatory continuum hypothesis (Maschinski and Whitham 1989). Despite being a well-developed general ecological theory, our understanding of the impact of cervids on understory vegetation is often derived from localised studies and with a single herbivore species, therefore the generality of forest floor vegetation responses across different species and strategies (i.e. mixed feeders versus browsers) of herbivores and different forest types and managements remain uncertain.

In Fennoscandian boreal forest ecosystems, two of the most abundant large-herbivores are two deer (Cervidae) species with contrasting feeding strategies. These are the moose (European elk) *Alces alces* and the red deer *Cervus elaphus*. Both species have largely increased in density and expanded in distribution, but differ in distribution. The moose is widely distributed in the forests of Fennoscandia, whilst the red deer is mainly found in southern and western areas. The moose is a typical browser and mainly forages on woody species throughout the year. Red deer are classified as mixed feeders, as they mainly select graminoids and herbs during summer, but browse during the winter season (Mysterud 2000). Both species have a long-term history in Norway (the region of this study, Rosvold et al. 2013) but have undergone recent population expansions over the past 50 to 60 years (Australheim et al. 2011). These two species are assumed to have the highest impact on biodiversity in the field-layer in different aged forests. Moose often use open areas such as clear-cuts for foraging (Bjørneraas et al. 2012) so impact on early-succession forests are likely to be strongest. Red deer are dominant along the west coast of Norway where there is less coniferous forest, hence clear cuts do not play such an important role in foraging and red deer impact biodiversity in more mature forests (Godvik et al. 2009).

Here we use a regional-level enclosure design to investigate the short term (four years) impact of moose and red deer on the physical and ecological structure of vascular plant vegetation in a range of forest types, in 51 sites distributed across central and southern Norway and differing in management, productivity and dominant cervid species. Specifically, we investigate the influence of moose in clear-cut forests and red deer in mature boreal forests; this distinction reflects the different habitat utilisation patterns of the different cervid species. Our main aim is to determine whether there are any general patterns in forest-floor vegetation response to herbivory across two different Cervidae species which largely utilise boreal forests differing in successional stages and tree composition, and forests differing in productivity (note that we do not seek to test differences between red deer herbivory and moose herbivory). We test the following predictions: P1a: total vascular plant density increases with succession in the clear-cut forests, with no temporal change in the mature forests. P1b: the increase in vegetation density is greater within exclosures than outside, with no enclosure effect in the mature forests. P1c: we expect a stronger treatment effect on vegetation density in less productive stands compared to more productive stands, due to greater potential for compensatory growth in productive stands. P2a: we predict that field layer vegetation height increases in clear cuts over time, but not in mature forests. P2b: field layer height is predicted to be greater in exclosures than outside exclosures in all types of forest. P3: vascular plant diversity is predicted to be stable in following exclusion of cervids in the short-term. P4: we predict that there will be an increase in relative density of grazing-sensitive species inside exclosures, but not outside of exclosures, across all forest types.

**Methods**

Our study covered four separate regions, with between 10 and 16 sites in each region (Fig. 1). In two of these regions the moose is the dominant cervid (Trøndelag and Telemark, Table 1) while in the other two regions the red deer is the dominant cervid (Tingvoll and Gloppen, Table 1). Densities are given in terms of metabolic biomass to account for the differing size and consumption rates of the different cervid species (Australheim et al. 2011). Although the level of cervid herbivory in the red-deer regions is higher than in the moose regions (Table 1), the red deer also utilise agricultural land (Godvik et al. 2009), so the actual utilisation of forest habitats is not necessarily higher. In the moose-dominated regions where rejuvenating stands within clear-cuts are greatly utilised, we selected sites (15 sites in Trøndelag, 16 in Telemark) within recently clear-cut stands in more productive spruce forests (of the bilberry or small-fern forest types, Moen 1999, *n* = 16), or less productive pine forests (of the cowberry–bilberry forest type, ibid, *n* = 15, Fig. 1). The clear cut forests were cut 10 years or less before enclosures were set up, and some were replanted with either pine, spruce or both (see Speed et al. 2013a for further details). In the red deer-dominated regions, where mature forests are greatly utilised by red deer, we selected sites (10 sites in each region) within mature stands of productive deciduous forests (of small-fern or tall herb birch forest types, Moen 1999, *n* = 13), or less productive pine forests (of heather–bog–bilberry–pine forest type, ibid, *n* = 7, Fig. 1). Forest productivity was included a priori in the study design stratifying sites within region between forest types and stands differing in productivity through differences in edaphic properties such as nutrient availability as well as climate and management history (Supplementary material Appendix 1 Table 1). Our study aims to investigate the
Figure 1. Location of experimental exclosure sites in two moose-dominated regions of Norway (Trøndelag, n = 15 and Telemark n = 16; recently clear-cut stands) and two red deer-dominated regions (Tingvoll and Gloppen, n = 10 for each; mature forests). Different symbols denote different forest types.
An interaction between time and exclusion treatment to investigate whether cervid herbivory influenced successional processes in the field layer. Density was analysed within growth form groups (herbs, graminoids, shrubs (all woody plants including dwarf shrubs and tree seedlings and saplings) and pteridophytes) as well as in total. We used mixed-effect models, using the R package ‘nlme’ (Pinheiro et al. 2013), fitting site as a random effect. For analyses of individual species’ responses we calculated the change in relative abundance over four years following exclosure. Effect sizes (standardised mean difference) were estimated, as the difference in the mean change in relative abundance between the unexclosed and exclosed treatments, standardised by the pooled standard deviation. Effect sizes were not estimated for rare species (those with initial relative abundances of less than 0.05 of total intercepts in the baseline data for each forest type). All analyses were performed separately for each forest type (i.e. spruce and pine forests in moose-dominated regions and deciduous and pine forests in red deer-dominated regions).

**Results**

**Vegetation structure**

The total vegetation density, as estimated by the total number of pin-point intercepts (Fig. 2), and height (Fig. 3) of vascular plants in the field layer increased over time in the spruce and pine clear-cut forests in the moose-dominated regions (as predicted, P1a). Vegetation density and height also increased over time in the deciduous forests in the red deer regions (contrary to predictions). Total vegetation density and height were greater in the more productive spruce forests than the less productive pine forests (Fig. 2, 3).

In the clear-cut pine forests, the increase in total vegetation density was greater where exclosed from cervid herbivory (supporting P1b, with an increase in total intercepts of 154%) than where exposed to cervids (124%, F_{1,865} = 5.2, p = 0.02, Fig. 2b), whilst the increase was equal between treatments in the spruce forests (supporting P1c, Fig. 2a). Total vegetation density was not related to treatment in the mature forests in the red deer regions (Fig. 2c–d), although it did tend to increase over time in the deciduous forests, both within and outside of exclosures (Fig. 2c, p = 0.06, contrary to P1c), but not in the mature pine forests (supporting P1c). Vegetation density did not tend to be greater in the more productive deciduous forests than in the pine forests (Fig. 2c–d). There was no difference in temporal trend in vegetation density between treatments in either the mature deciduous or pine forests browsed by red deer (Fig. 2c–d). There was a greater increase in estimated shrub canopy density where exclosed than unexclosed in the deciduous forests browsed by red deer (Fig. 2c, F_{1,865} = 4.81, p = 0.03), but the interaction between time and treatment was not significant (at p < 0.05) for any other functional group or forest type (Fig. 2a–b,d).

Field-layer vegetation height (expressed as the median height of 16 points within each quadrat) increased over time in the moose-dominated spruce and pine forests (Fig. 3a–b, supporting P2a), and in both forest types the increase was significantly greater inside than outside of the cervid

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**Table 1. The density of forest cervids in each of the four regions during the study period. To standardise for the different sizes of the three forest cervid species densities are expressed as metabolic biomass km⁻², following the methods presented by Austrheim et al. (2011). Densities are estimated at the municipality scale, for the municipalities within each region where exclosures have been initiated (n municipalities = eight for Telemark, nine for Tørendal and one for each of Gloppen and Tingvoll). Standard errors are thus only shown for the moose regions (in parentheses).**

<table>
<thead>
<tr>
<th>Region</th>
<th>Main cervid</th>
<th>Moose (kg km⁻²)</th>
<th>Red deer (kg km⁻²)</th>
<th>Roe deer (kg km⁻²)</th>
<th>Total (kg km⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gloppen</td>
<td>red deer</td>
<td>0</td>
<td>229.6</td>
<td>0</td>
<td>229.6</td>
</tr>
<tr>
<td>Tørendal</td>
<td>moose</td>
<td>71.2 (6.1)</td>
<td>103.3 (3.1)</td>
<td>12.5 (3.6)</td>
<td>190.8</td>
</tr>
<tr>
<td>Telemark</td>
<td>moose</td>
<td>69.3 (9.9)</td>
<td>2.1 (0.8)</td>
<td>8.8 (2.9)</td>
<td>80.1 (11.9)</td>
</tr>
</tbody>
</table>

At each site, two 20 × 20 m plots were established in homogenous stands. These were a minimum of 20 m and a maximum of 50 m apart to avoid edge effects and minimise heterogeneity. One of the two plots was randomly assigned as an exclosure, and the other as an unexclosed plot. Exclosures were constructed with 3 m tall wooden stakes sunk into the ground. Mesh wiring was used to exclude cervid herbivores, and a top strand was added at around 2.5 m height. The exclosures were erected in 2006 for seven of the sites in Gloppen, in 2008 in Tørendal, Tingvoll and the remaining three sites in Gloppen, and in 2009 in Telemark. Exclosures did not prevent access of rodents or the mountain hare *Lepus timidus*. Roe deer *Capreolus capreolus* are also present at many of the study sites, but only at low density (Table 1), hence this study is framed in terms of the dominant cervid species for each region.

In each plot (exclosed and unexclosed), 10 permanent (fixed-location) quadrats of 50 × 50 cm were established at randomly selected locations. Base-line vegetation data were recorded during the summer immediately prior to the erection of exclosures. The quadrats were re-assessed two and four years after exclosure. Assessment of the field layer was carried out using a point-intercept method (Jonasson 1998), with 16 regularly spaced pins per quadrat. All vascular plant intercepts with each pin were recorded to species level. The height of the top intercept per pin was also recorded. The total number of vascular plant hits per quadrat (i.e. summed across 16 pins) was used as an estimate of total vegetation canopy density. This is a measure similar to the vegetation area index (Wilson 2011). The median of the heights of the top intercept of the 16 pins was used as an estimate of field-layer vegetation height. Vegetation sampling was based on point-intercept sampling, and not exhaustive surveys. Therefore diversity was analysed in terms of Simpson’s index since this index reflects the variation in the species abundance distribution (Magurran 2004).

Data was analysed in the R statistical environment. For analysis of height, plant density and diversity we tested for an interaction between time and exclusion treatment to
exclosures (supporting P2b). In both the spruce and pine forests the average field layer vegetation height approximately doubled over four years where moose had access, but trebled over the same time period where moose were excluded (Fig. 3a–b). In the red deer-dominated regions the same pattern, of a greater height increase in the absence of cervids, albeit of a lower magnitude, was evident in the deciduous forests (Fig. 3c, contrary to P1c), but in the pine forests there was no change in height, nor difference between treatments (Fig. 3d, supporting P1c).

**Community structure**

Diversity, as measured by Simpson's diversity index increased over the four year time period in both spruce and pine forests in the moose-dominated clear-cuts and the
pine forests in the red deer-dominated regions (partly supporting P3, Fig. 4a–b, d), but not in the red deer domi-
nated deciduous forests (Fig. 4c). The interaction between
time and exclosure treatment in determining diversity was
not significant in any region or forest type, although there
was a weak tendency for a greater increase in diversity
within the exclosures in the moose dominated pine
forests.

The change in relative density within the field-layer (P4) of Sorbus aucuparia, Epilobium angustifolium and
Chamaepericlymenum suecicum was more positive inside the
exclosures than outside the exclosures in the moose-
dominated spruce forests, whilst there was a decrease in the
relative density of Populus tremula inside the exclosures
(Fig. 5a, Supplementary material Appendix 1 Table 2a). In
the moose-dominated pine forests, Calluna vulgaris and
Avenella flexuosa had both increased in relative density
inside the exclosure (Fig. 5b; A. flexuosa decreased in
relative density outside the exclosure Supplementary
material Appendix 1 Table 2b), and Vaccinium myrtillus
decreased in relative density inside the exclosures but
not outside (Fig. 5b, Supplementary material Appendix
Table 2b).

In the deciduous forests where red deer are the dominant
cervid, Vaccinium myrtillus increased in relative density
inside the exclosures, but not outside whereas the herb
Potentilla erecta and the grass Holcus mollis decreased in rela-
tive density inside the exclosures but not outside (Fig. 5c,
Supplementary material Appendix Table 2c). No species
showed a more positive change in relative density outside
the exclosures than inside the exclosures in the red
deer-dominated regions’ deciduous forests (Fig. 5c), but the
grazing-resistant grass Molinia caerulea showed this pattern
in the pine forests (Fig. 5d, decreasing inside the exclosures
but increasing outside). Vaccinium vitis-idaea decreased in
relative density more outside the exclosures than it did inside
the exclosures (Fig. 5d, Supplementary material Appendix 1
Table 2d).

Discussion

High and increasing densities of moose and red deer are
relatively recent phenomena in many boreal forests (Côté
Despite clear evidence that forest cervids can have profound

Figure 3. Average height (median of 16 pins per quadrat) of the field-layer inside and outside of exclosures in moose-dominated regions
and red deer-dominated regions, stratified by forest type (spruce (a) and pine (b) in the moose regions, and deciduous (c) and pine
(d) in the red deer-dominated region) and length of time since the exclosures were erected. Mean and standard errors are displayed,
estimated from mixed effects models fitting site as a random intercept. Likelihood ratio (ANOVA) output tables are shown in inset tables,
with estimates from the mixed effect model for the intercept (I) and the variables exclosure treatment (E), time in years since exclosures
were erected (T) and the interaction between exclosure treatment and time (E:T).
Figure 4. Simpson diversity of the field layer within 50 × 50 cm plots inside and outside of exclosure in moose-dominated regions and red deer-dominated regions, stratified by forest type (spruce (a) and pine (b) in the moose regions, and deciduous (c) and pine (d) in the red deer-dominated region) and length of time since the exclosures were erected. Mean and standard errors are displayed, estimated from mixed effects models fitting site as a random intercept. Likelihood ratio (ANOVA) output tables are shown in inset tables, with estimates from the mixed effect model for the intercept (I) and the variables exclosure treatment (E), time in years since exclosures were erected (T) and the interaction between exclosure treatment and time (E:T) for the total species richness.

influences on forest vegetation (Horsley et al. 2003, Hester et al. 2006, Nuttle et al. 2013), the use of experimental approaches to investigate the influence of these ungulates on understory vegetation are usually highly localised in focus (Hester et al. 2000). Comparing effects of contrasting large herbivores on both vegetation and plant community structure among forest types in different regions and with varying productivity (shown in a conceptual model in Fig. 6), we see that the most susceptible parameters to cervid exclusion in the short-term are field-layer height and the abundances of individual species, whilst total field-layer canopy density and diversity measures generally do not vary following cervid exclusion in the short-term, as predicted. Cervid exclusion had a lesser effect on understory vegetation in mature forests with red deer than clearcuts with moose, highlighting the interaction between cervid herbivory and forest succession which likely acts through light availability (Kielland and Bryant 1998, Hidding et al. 2013, Speed et al. 2013a). Our study highlights the ecological contingencies that add complexity to our general theoretical understanding of the impact of herbivores on forest understory vegetation.

Our study is clearly short-term and long before any ‘stable state’ may be reached following exclusion of herbivory in these different forest areas and it provides clear indications of those parameters which respond faster than others. In the short term there is a strong influence of cervid herbivory on field-layer vegetation in clear-cut forests that are under strong successional dynamics, and where light is not limiting. Independent of light levels, the rate of vegetation response is also likely to be affected by productivity. Habitat productivity has shown to be an important predictor for modelling effects of herbivory on plants and vegetation (Proulx and Mazumder 1998, Persson et al. 2007). We had expected that vegetation density would show a greater increase inside the exclosure in the more productive forests than the less productive forests, in accordance with the compensatory continuum hypothesis (Maschinski and Whitham 1989). However, contrary to this prediction, vegetation density increased within exclosures only in the...
Figure 5. Standardised mean differences in the change in relative abundance of field-layer species between unexclosed and exclosed vegetation, over a four year period following exclosure. Data are shown within spruce (a) and pine (b) forests in the moose-dominated regions, and deciduous (c) and pine (d) forests in the red deer-dominated regions. A positive outcome denotes a greater increase (or lower decrease) in relative abundance of that species where unexclosed and a negative outcome denotes a greater increase (or lower decrease) in relative abundance inside the exclosures. Only species that comprised over 0.5% of pin-point intercepts in the baseline data for each forest type are shown. Species are ordered with those becoming more dominant inside the exclosures at the bottom. Points show the estimated effect size, and the arrows show the 95% confidence interval of the effect size. Note the different numbers of species per forest type and the vertical line showing the location of a null effect. The actual changes in relative abundance (rather than differences between treatments) are shown in Supplementary material Appendix 1 Table 2.

less productive clear-cut pine forests in the moose-dominated regions. This suggests that the vegetation in the less productive pine forests is more responsive to cervid exclusion than in the more productive spruce forests. On the other hand, there were some temporal changes in vegetation independent of exclosure treatment in the mature forests (for example an increase in total vegetation density in the deciduous forests and an increase in diversity in the pine forests), indicating that the vegetation in these mature forests is still changing over time. Productivity at a finer scale than forest stands may be important in the context of forest field-layer vegetation response to herbivory within the compensatory continuum hypothesis.

Vegetation physical structure was more responsive than community structure, indicating as expected that changes in relative abundances are relatively slow compared to change in total abundance following a short-term decrease in herbivory (Austrheim et al. 2008). This is in agreement with browsing effects on species in the tree layer where the main impact of browsing was found to be on tree height growth and no effect on tree species composition was found (Speed et al. 2013). However, there were also some responses at the species level, and these varied between forest types and the dominant cervid species. For example, Vaccinium myrtillus became more dominant where browsed in the moose-dominated pine forests, and less dominant where browsed in the red deer-dominated deciduous forests. This is likely a result of the different feeding strategies of the two cervids (Mysterud 2000): red deer are mixed-feeders and forage on V. myrtillus, hence the decrease in the red deer regions, whilst moose are more strict browsers, so V. myrtillus may benefit from changed competitive interactions following moose browsing on the taller tree and shrub layers. Furthermore, V. myrtillus may be more tolerant of browsing under the higher light levels found in clear-cut forests than in the mature forests (Hester et al. 1991).

Understory plant species richness has been shown to increase with red deer density in boreal forests in western Norway (Hegland et al. 2013). However, the pattern of plant diversity change along a gradient of increasing red deer...
density has been shown to vary between functional groups, with for example a decrease in dwarf shrub richness and an increase in graminoid and moss species richness (Hegland et al. 2013). Although our study did not show changes in plant diversity, it was of short duration. We did however observe contrasting patterns in the relative abundance of functionally similar species to cervid exclusion. For example *Sorbus aucuparia* showed a more positive change in relative abundance inside the exclosures in the moose-dominated spruce forests, whilst *Populus tremula* showed the opposite pattern in the same forest type. Both of these species may be heavily browsed by cervids at the seedling stage, and both can reproduce through vegetative mechanisms as well as seeds (Myking et al. 2011, 2013). However, *S. aucuparia* is more tolerant of shade (Myking et al. 2013), thus the decrease in *P. tremula* within the exclosures may be due to increased shading by over-story trees caused by a lack of browsing. Indeed, *S. aucuparia* trees also showed a greater increase outside than inside the exclosures in red deer forests, a pattern that may be associated with snow cover (Speed et al. 2013b).

There was a shift in growth-form composition between the exclosed and unexclosed vegetation. As expected, shrubs showed a positive response to cervid exclusion, with an increase in species richness in exclosures in the less productive pine forests in the clear-cut moose regions and an increase in canopy density in exclosures in the more productive red deer-dominated mature deciduous forests. Graminoid species richness decreased within the exclosures in the less productive pine forests, whilst neither herb abundance nor species richness varied with cervid exclosure, also as expected. A previous meta-analysis highlighted the variation in response to herbivory across resource levels in different growth forms in plants (Hawkes and Sullivan 2001), identifying that shrub and herb growth following herbivory was higher under low resources whilst graminoid growth following herbivory was greater under high resources. This difference shows the importance of including plant growth forms when considering vegetation response to herbivory. 

Vegetation responses to herbivory across forest types also varied within individual species: in less productive forests *Avenella flexuosa* becomes more dominant in the absence of cervid herbivory, while in the more productive forests, more competitive graminoids and herbs (e.g. *Epilobium angustifolium* in the moose-dominated regions and *Holcus mollis* in the red deer-dominated regions) increase in relative abundance whilst *A. flexuosa* decreased in relative abundance in the absence of cervids. Whilst graminoids have been found to increase in response to white-tailed deer density (Tremblay et al. 2006) and simulated moose browsing (Mathisen et al. 2010), our results highlight how the response of vegetation to cervid herbivory is multi-faceted, being influenced by factors such as species composition, herbivore selectivity, competition from other understory vegetation, forest productivity and interactions with the tree layer, which itself is impacted by cervids. This is consistent with...
the patterns reported by others, that the response of many species to grazing is highly context dependent, particularly with regard to productivity and neighbouring species (Palmer et al. 2003, Pakeman 2004).

Conclusions

In this study we have demonstrated both generic and specific responses of boreal forest field layer vegetation to cervid herbivory even over short timescales. We found that field-layer height and abundances of individual plant species were generally more susceptible than field-layer density and diversity to cervid exclusion in the short-term, across forest types and herbivore feeding strategy. However, different boreal forests varied in their responses to cervid exclusion, with vegetation in clear-cut forests utilised by moose appearing to be more susceptible overall than vegetation in mature forests utilised by red deer. We found no strong evidence for forest productivity being a predictor of forest field-layer vegetation susceptibility to cervid herbivory.

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Supplementary material (available online as Appendix oik.01373 at <www.oikosjournal.org/readers/appendix>). Appendix 1.